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Do dense layers of invasive plants elevate the foraging intensity of small mammals in temperate deciduous forests? A case study from Pennsylvania, USA

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Abstract

Monospecific stands of invasive plants can dramatically restructure habitat for fauna, thereby elevating population densities or promoting foraging of consumer species who benefit in the altered habitat. For example, dense stands of invasive plants may protect small mammals from predators, which in turn could increase foraging pressure on seeds that small mammals feed upon. We used a before-after, control-impact experimental design to test whether small mammal capture rates were higher and giving-up densities (GUDs) lower beneath dense stands of *Berberis thunbergii*, an invasive shrub with a rapidly expanding range throughout eastern North America. Our experimental design included three plot categories: 1) plots heavily invaded by *B. thunbergii*, 2) control plots lacking invasive shrub cover, and 3) invaded plots where we eradicated *B. thunbergii* midway through the study. Although our overall small mammal capture rate was low, small mammal captures were 65% higher in *B. thunbergii* invaded habitat relative to control plots and eradication lowered capture rates by 77%. GUDs were also 26% higher within *B. thunbergii* relative to control plots and eradication decreased GUDs by 65%. Our findings suggest that small mammals perceive dense stands of *B. thunbergii* as relatively safe foraging habitat. Prior surveys within our study locations revealed dramatically depressed tree seedling densities under *B. thunbergii*, thus invasive plants may promote intensive foraging by small mammals and reduce recruitment for species with foraged seeds or seedlings.

Keywords

Berberis thunbergii, foraging, giving-up density, recalcitrant understory, small mammals

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Introduction

Nonnative plant species that become invasive frequently form dense, nearly monospecific layers that can cause substantial declines in native plant species abundance and diversity. One mechanism that may underlie these declines is that invasive species may commonly provide privileged foraging areas, whereby vertebrate seed and seedling predators gain refuge from their enemies (Orrock et al. 2009; Orrock et al. 2015; Guiden and Orrock 2017). Thus, seed predation by small mammals may be much greater beneath dense layers of invasive plant species than in nearby uninvaded patches. Consequently, any reduction in the diversity and abundance of native plant species could be caused by habitat-mediated predation rather than interspecific resource competition between exotics and natives (e.g., Royo and Carson 2005, 2008; Durra et al. 2011). For example, both experimental (Dutra et al. 2011) and observational (Mattos et al. 2010) studies have demonstrated that dense layers of the invasive Amur honeysuckle (*Lonicera maackii*) protected small mammals from predators, thereby resulting in elevated foraging event frequencies.

Habitat-mediated predation may be a common phenomenon throughout eastern North American forests because many common invasive plant species are understory shrubs or small trees known to form dense stands (see reviews by Royo and Carson 2006; Richardson and Rejmánek 2011). Common invasive trees or shrubs include several species of honeysuckle (*Lonicera* spp.), glossy buckthorn (*Rhamnus cathartica*), Chinese privet (*Ligastrum sinense*), autumn olive (*Eleagnus umbellata*), burning bush (*Euonymus alatus*), and Japanese barberry (*Berberis thunbergii*) among several others. Elevated seed predation has been well-investigated beneath dense stands of native species, however, whether dense understory layers of invasive shrub species typically create preferred habitats for small mammals remains unclear because there are too few studies to draw any firm conclusions (Orrock et al. 2015). Moreover, non-native species may lead to declines in small mammals if they provide fewer seed resources compared to the native species they displaced. Here, we focus on one of the most widespread and pernicious invaders, Japanese barberry, and evaluate whether barberry creates privileged foraging grounds across three different urban forests using a rigorous BACI experimental design (see below).

Japanese barberry (*Berberis thunbergii*, hereafter referred to as barberry) is a woody shrub native to East Asia that represents a key model species for investigating cascading effects of invasive, shrubs. Barberry was introduced to North America in the late 19th century and has spread to at least 32 U.S. states and 6 Canadian provinces (USDA, NRCS 2017). The shrub often forms dense stands that cause both structural and functional shifts in forest understories (Clark and Seewagen 2019). Recalcitrant barberry stands typically reduce temperatures and increase humidity, soil pH, and available soil nitrate relative to uninvaded areas (Kourtev et al. 1999, 2003; Williams and Ward 2010; Link et al. 2019). As with many invasive shrubs (Collier et al. 2002; Flory and Clay 2010), dense barberry patches are often associated with precipitous declines (>33% for certain species) in the abundance of native flora (Kourtev et al. 1998). Si-

lander and Klepeis (1999) attributed declines in native species to interspecific competition for light, however, they did not consider if seed and seedling predators might be partly responsible. At two of our study locations (see below), Link et al. (2018) found a dramatic reduction (82%) in native tree seedling density beneath barberry canopies. They hypothesized that these reductions may have been due to seed predators because tree seedlings transplanted under barberry canopies, thus bypassing the vulnerable seed and small seedling phase, grew at similar rates relative to those planted in nearby controls (Link et al. 2019). Williams et al. (2009) did not detect higher small mammals' capture rates beneath barberry patches but they focused on only a single target species rather than entire small mammal assemblages. Nonetheless, a few studies suggest that the presence of invasive shrubs (such as *Rhamnus cathartica* and *Lonicera maackii* in North America) promotes small mammal foraging activity (Orrock et al. 2015, Guiden and Orrock 2017, Guiden et al. 2019).

Here, we tested the hypothesis that small mammals would be more abundant beneath dense barberry patches or would forage longer in these patches or both. We quantified foraging intensity by estimating giving-up densities (GUDs), defined as the proportion of seeds consumed when mixed with an inorganic substrate (Bedoya-Perez et al. 2013). We predicted that 1) small mammal capture probability would be higher beneath dense patches of barberry, 2) experimental removal of barberry would decrease the capture of small mammals, 3) GUDs would be lower in patches that lacked a dense canopy of barberry or where barberry had been removed, and 4) our results would not vary significantly among three forest reserves separated fairly widely in space. The latter prediction goes to the issue of generality and, if true, suggests that our results are less likely to be location-specific. We used a before/after, control/impact (BACI) experimental design where patches of dense barberry were cleared midway through our field season to assess if removing an invasive regulated the foraging of vertebrate seed predators.

Methods

Plot selection

We conducted this study from May to September 2018 within closed canopy forest at three protected temperate forest reserves (hereafter referred to as locations) in southwestern Pennsylvania, USA: the Eden Hall campus of Chatham University (157 ha, 40.6638N, 79.9559W), Irwin Run Conservation Area (29.5 ha, 40.6242N, 80.0053W), located about 9.6 km from the Eden Hall campus, and Latodami Nature Center (101.1 ha, 40.6207N, 80.0297W) located about 11 km from Eden Hall (Fig. 1). The forests are within proximity to mixed-use residential zones in the suburban Pittsburgh metropolitan area. All three locations consisted of second growth deciduous forest interspersed variously with patches of coniferous forest, agricultural land, and urban land cover (Link et al. 2018). Canopy tree species at each location consisted primarily of *Quercus* spp., *Prunus serotina*, *Sassafras albidum*, *Acer rubrum*, and *Carya* spp.

Urban forests throughout this region are characterized by overbrowsing due to high densities of white-tail deer (Carson et al. 2014). Invaded and removed plots did not differ significantly in barberry density or biomass among the invaded and pre-removal plot types (Appendix 1: Fig. A1).

Experimental design

Our experiment used a before/after, control impact (BACI) design with small mammal captures and foraging behavior assessed as dependent variables in the presence versus absence of barberry. We had three plot types at all three locations: plots with a dense understory layer of barberry throughout the sampling period (hereafter invaded plots), plots where barberry had been manually removed midway through the field season with observations made before and after removal (hereafter removal plots), and nearby control plots lacking a contiguous barberry understory. We only used barberry patches containing ≥ 50% areal cover of barberry, which commonly occurred at all three study locations and elsewhere throughout much of the invasive range of barberry (Ward et al. 2009, Ward and Williams 2011). Before establishing our plots, we surveyed barberry patch boundaries by walking the perimeter of contiguous barberry patches with a GPS. Mean (± 1 standard deviation) patch size was 2009 ± 3211 m^2, with the largest patch size (9653 m^2) at the Eden Hall location and the smallest patch size (13 m^2) at the Irwin Run location (Fig. 1). Sixty total plots were distributed throughout the three locations: five of each plot type at Irwin Run and Latodami, and ten of each plot type located at Eden Hall. Plots were randomly chosen, spaced a minimum of 5 meters apart, and positioned at least 5 m from obvious habitat features that might affect mammal behavior, such as concentrations of large woody debris (Fig. 1). Invaded and removed plots were positioned approximately 5 m within the boundary of a barberry patch. Control plots were randomly selected 10–50 m away from barberry patches but lacked a dense barberry layer.

The removal plots were surveyed as invaded plots until midway through the field season when we removed barberry using a mechanical pole saw from July 16th to July 20th, 2018. A square, 25 m^2 area centered on the plot location was entirely cleared of barberry at removal plots. We did not leave trap or use seed trays for one week immediately after barberry removal then, resumed sampling as before. We quantified barberry density and stem diameter within two randomly selected positions immediately adjacent to invaded and removed plot points using a 1 m^2 grid. We used stem diameters to estimate barberry aboveground biomass allometrically using equations from Link et al. (2018).

Small mammal trapping

We used Sherman live traps (50.8 mm × 63.5 mm × 165.1 mm) to quantify capture rates (Yahner 1992, Royo and Carson 2008). On trap dates, a single trap was deployed in all 60 plots at all locations and was baited with a peanut butter/oatmeal/

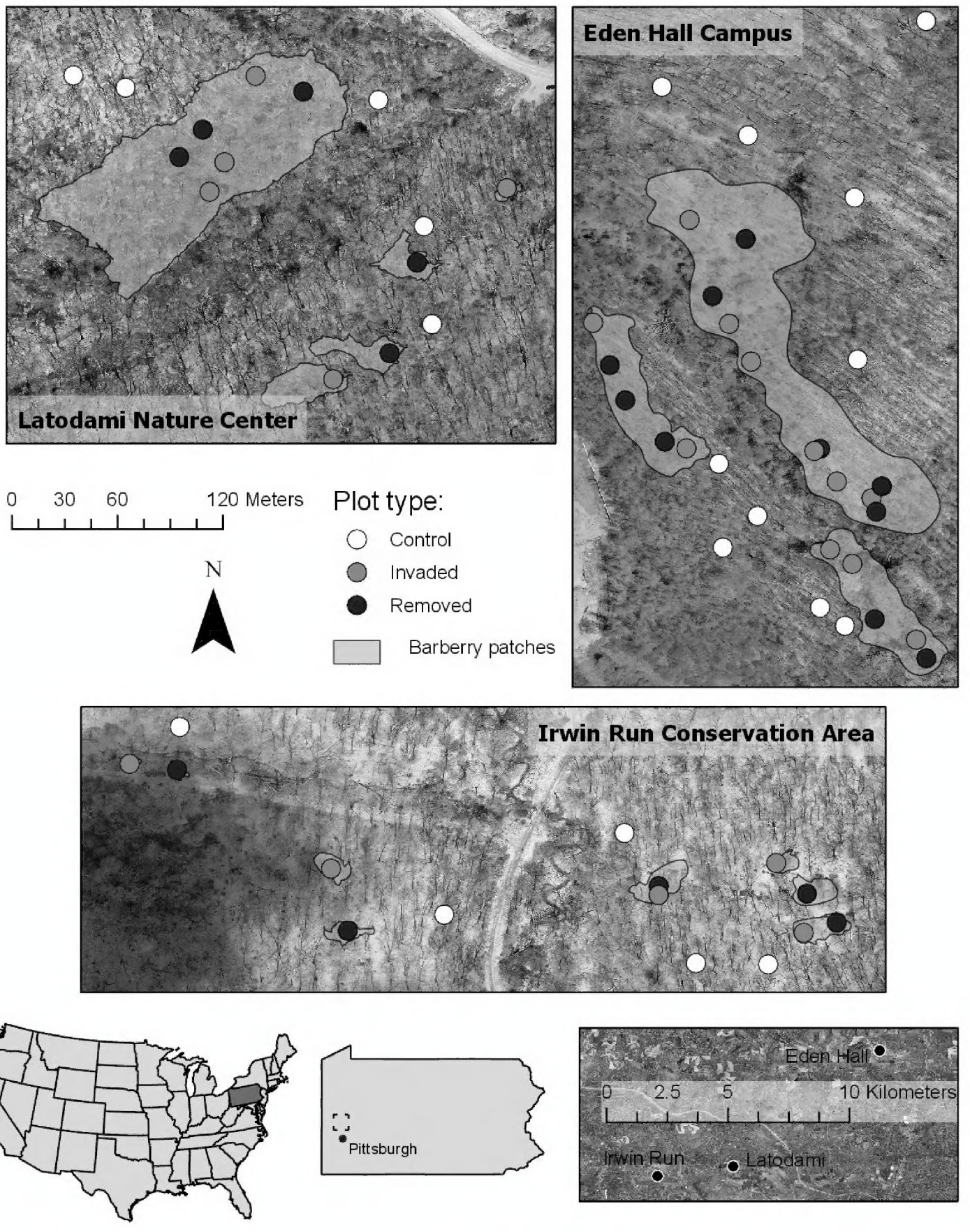

Figure 1. Map of study locations, barberry patches, and approximate positions of plots. The three detailed location maps are illustrated at the same spatial scale. Plot positions were randomly selected within 5 m of the barberry patch perimeters and away from idiosyncratic habitat features (such as downed tree crowns). Points show the approximate positions within 6 m, because the overstory canopy or topographic features or both reduced the accuracy of global positioning systems.

gelatin mixture (Yahner 1992, Royo and Carson 2008). Gelatin was used to preserve shape and consistency. Traps were set for 3–4 consecutive days every other week in June, July, and August (660 trap nights) and checked approximately every 12 hours.

We weighed and identified all captured mammals then released captive individuals, unmarked, adjacent to each plot. Small mammal capture protocols were approved by the Institutional Animal Care and Use Committee of Chatham University in accordance with the American Society of Mammalogists' guidelines for the use of wild animals (Sikes 2016). Disturbed or damaged traps were omitted from subsequent analyses. By the end of the field season, 491 evenings' worth of data were obtained across all plots and locations.

Giving up densities

We used seed buckets placed within each of the 60 plots deployed over 24-hr periods every other week throughout the field season to quantify GUDs of small mammals (Jacob and Brown 2000, Mattos and Orrock 2010). Seed bucket deployment weeks alternated with live trapping weeks to ensure that the two metrics did not conflict with each other. Seed buckets were 3.8-liter translucent round plastic containers with detachable lids (Jacob and Brown 2000; Mattos and Orrock 2010). Two 5 cm diameter holes were cut into opposite sides of the containers about 1 cm from the bottom to allow small mammal access (Mattos and Orrock 2010). Buckets were covered with a lid to prevent seed predation by birds or cervids and loss of contents from inclement weather (Mattos and Orrock 2010; Jacob and Brown 2000; Mattos and Orrock 2010). Each bucket received 6 grams of millet mixed with 200 mL of commercial play sand (Jacob and Brown 2000; Mattos and Orrock 2010). Following deployment, the millet and sand mixture was dried at 100 °C for 3 hours (to facilitate separation), the remaining millet was sieved from the sand, and weighed to evaluate foraging rate as a percentage of seed remaining (following Brown 1988). We deployed seed buckets at each location twice prior to the barberry removal dates and twice after the removal date. We removed replicate buckets that had been disturbed (15.5%) from subsequent analyses. By the end of the field season, 191 seed bucket evenings were recovered from all plots.

Statistical analysis

We assessed our findings using either linear or generalized linear mixed effect (GLMM) regression models. To avoid temporal pseudoreplication (Hurlbert 2013), our data were first divided into periods before and after the barberry removal and analyzed separately. Our dependent variables (captures and GUDs) were inherently not normally distributed. Therefore, capture probability was modeled using a GLMM with a binomial error distribution and with location as a fixed effect and plot as a random effect (to account for repeated measures). GUDs were analyzed by logit-transforming the proportion of remaining millet then averaging each GUD per plot. Averages were

assessed using a linear model with location and an interaction term between location and plot type included as fixed effects. Location and an interaction term was included as a fixed effect in models to 1) account for variability in dependent variables among locations but also to 2) allow for determination of whether dependent variables varied among locations and, when that was the case, 3) if the effects of experimental treatments were consistent among locations. All statistical analyses were conducted in R version 3.5.2 (R Foundation for Statistical Computing 2019) and the GLMM model was assessed using the package *lme4* (Bates et al. 2019).

Results

We captured 23 small mammals in total: eight *Peromyscus leucopus*, ten *Peromyscus maniculatus*, four *Tamias striatus*, and a single *Blarina brevicauda*. Prior to the barberry removal treatment, capture probability significantly varied among the three study locations but not among experimental treatments (Table 1). However, during the period following barberry removal, capture probability was marginally statistically significantly different among treatments, with capture probability elevated in invaded plots relative to control and treatment plots (Table 1, Figure 2A). Before barberry removal, GUDs varied among study locations but not treatments (Table 1, Figure 2B). Following barberry removal, GUDs declined overall and did not vary among locations but values were statistically significantly greater in invaded plots relative to control and barberry removal plots (Figure 2C). No models included statistically significant terms for interactions between treatment and location.

Table 1. Results of linear and generalized linear mixed models predicting dependent variable responses to experimental treatments and plot location. Linear models correspond to F-values while generalized linear models report χ^2-values.

Model	Before or after barberry removal	Term	F- or χ^2-value $_{(df)}$	p-value
Giving- up density linear model, logit-transformed	Before	Location	$7.7_{(2,50)}$	0.0012
		Treatment	$1.0_{(2,50)}$	0.3425
		Interaction	$0.6_{(4,50)}$	0.6894
	After	Location	$0.2_{(2,50)}$	0.7922
		Treatment	$3.9_{(2,50)}$	0.0259
		Interaction	$0.5_{(4,50)}$	0.7004
Trap rate generalized linear mixed model	Before	Location	$0.3_{(2)}$	0.3014
		Treatment	$2.4_{(2)}$	0.8391
		Interaction	$0.2_{(2)}$	0.9933
	After	Location	$0.1_{(2)}$	0.9817
		Treatment	$4.7_{(2)}$	0.0946
		Interaction	$0.1_{(2)}$	0.9988

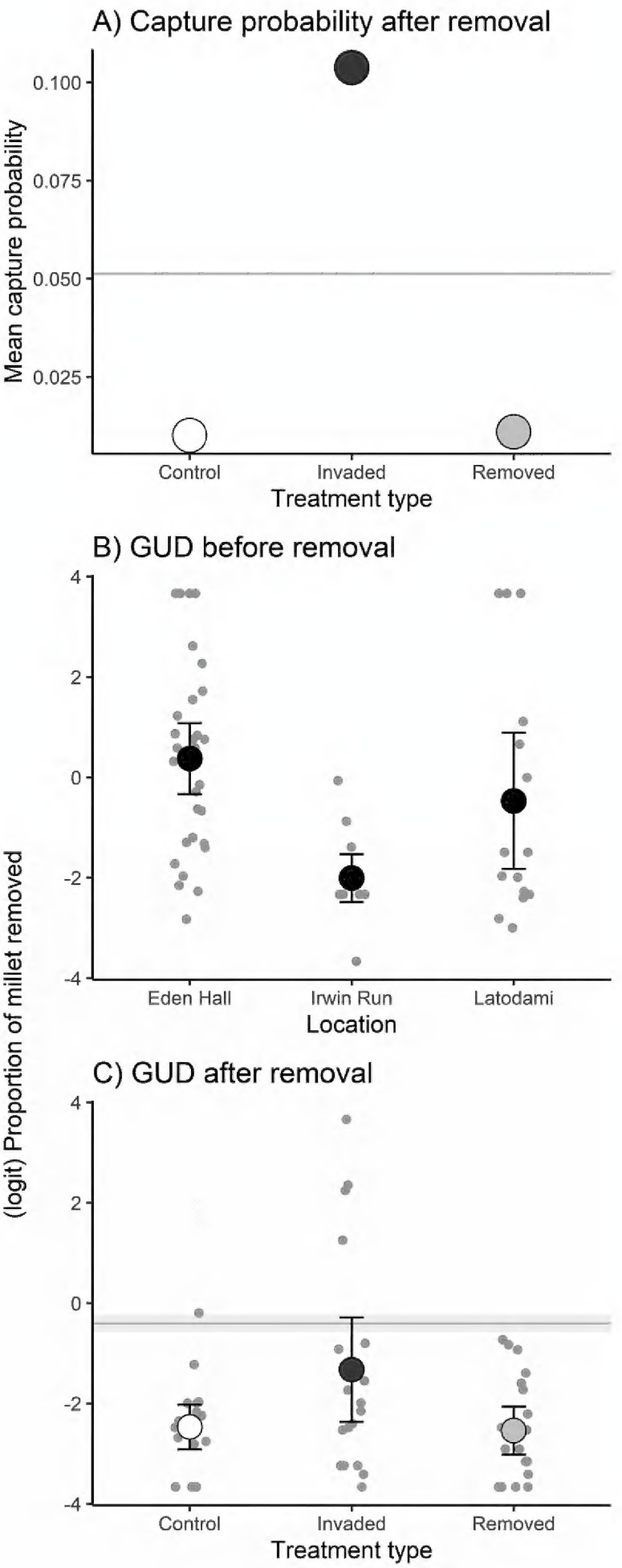

Figure 2. A Mean capture rates of small mammals during the period after experimental barberry removal delineated by plot type. The horizontal line illustrates the mean capture rate across all locations and treatments during the period prior to experimental barberry removal **B** mean (± 95% confidence intervals) giving-up densities delineated by location before the experimental barberry removal and **C** by treatment type for the period after barberry removal. The line and associated gray ribbon illustrate the mean ± 95% confidence interval for giving-up densities across all treatments and locations before barberry removal.

Discussion

Results affirmed our hypotheses and provide evidence that small mammals forage more aggressively under invasive shrub canopies. During the latter half of the field season, both the small mammal capture probability and GUDs were significantly higher in plots with recalcitrant barberry layers relative to both control plots and plots where barberry was removed. Differences in capture probability and GUDs were not detected in the first half of the field season and we observed a decrease in small mammal GUDs between early and late summer. However, comparable seasonal patterns in activity have been observed for at least *P. leucopus* in similar ecological settings elsewhere (McMurry et al. 1996). Although we cannot rule out the possibility that the activity of removing barberry itself altered the behavior activity of small mammals after the event, dependent variables in control plots lacking barberry were nearly identical to barberry-removed plots during the second half of the field season. Therefore, we conclude that small mammal foraging activity under barberry canopies is elevated relative to forest floors lacking the invasive species.

Dense patches of a suite of invasive shrub species are now widespread throughout much of the Eastern Deciduous Forest Biome of North American and often cause major declines in native plant diversity (see introduction). Research exploring the mechanisms behind these patterns to date has typically attributed declines in diversity to interspecific resource competition between nonnative shrubs and native species, biological or chemical changes to soil environments that occur after invasion, or invasive species-driven allelopathic effects (Hierro and Calloway 2003; Morales and Traveset 2009; Skurski et al. 2014). Our findings, and those of several others (Mattos and Orrock 2010; Dutra et al. 2011; Malo et al. 2013; Guiden and Orrock 2019) provide an alternative, though not mutually exclusive, explanation. Specifically, seed and seedling predation reduces flora diversity because small mammals occur more frequently and forage longer beneath dense shrub patches, thereby promulgating apparent competition (Holt 2017) between invasive and native flora. The phenomenon is not limited to nonnative taxa: indeed, dense understories of native shrubs and ferns also increase the activity of small mammals and levels of seed predation (Yahner 1986; Carey and Harrington 2001; Castleberry et al. 2002; Spencer et al. 2005; Royo and Carson 2008).

Nonetheless, nonnative shrubs may be more likely to create dense understory layers than native plant species because herbivores typically avoid them (Grosholz 2010; Averill et al. 2016). In our case, barberry may provide particularly effective cover from enemies because it has thorns and it grows via multiple stems that radiate densely from a central root crown (Gleason and Cronquist 1991; Ehrenfeld 1999). Overall, our results, combined with those of others, suggest that the spread of numerous nonnative shrubs across eastern forests, may increase predation pressure on vulnerable seeds and seedling across broad regions wherever these shrubs occur and are abundant. Because of ubiquity of invasive woody plants globally (Royo and Carson 2006; Richardson and Rejmánek 2011), our findings could apply beyond the eastern U.S., and call for replicated experiments in invaded areas worldwide.

Other mechanisms whereby nonnative shrubs increase the abundance or foraging activity of small mammal activity exist beyond providing dense cover. Invasive species may augment small mammal populations if they produce edible fruits and seeds (Orrock et al. 2015). In our case, barberry produces a fruit that is palatable to birds and mammals (Silander and Klepeis 1999; Hayes and Holzmueller 2012) and thus may be augmenting food resources. However, dense patches of invasive shrubs may not always enhance the abundance and foraging activity of small mammals (Hayes and Holzmueller 2012). For example, nonnative shrubs can reduce the abundance of native plant species that are key food resources, or the nonnatives displace native woody vegetation that provided better cover than the nonnative shrubs (e.g., large seeds; Lambrinos 2000; Ostoja et al. 2009; Freeman et al. 2014; Lucero and Callaway 2018). Overall, dense patches of nonnative shrubs can increase small mammal abundance or concentrate foraging because they provide dense cover, the cover extends earlier or later during the growing season, or the nonnatives augment food resources.

Prior investigations in our study locations have detected evidence that seed or seedling predation causes the low densities of native tree seedlings beneath barberry understories. Specifically, Link et al. (2018, 2019) bypassed the seed germination and early establishment phase by transplanting tree seedlings (> 20 cm tall) under barberry and within adjacent control areas lacking barberry. No differences in the survival or growth rates of *Quercus* spp. and *Prunus serotina* seedlings between barberry patches and control patches lacking barberry were detected, suggesting that vertebrate seed and seedling predators kill seeds or young seedlings, whereas larger individuals are less vulnerable, though alternative explanations cannot be ruled out (e.g., allelopathy). Still, Guiden and Orrock (2017) and Bartowitz and Orrock (2016) found that an invasive shrub (*Rhamnus cathartica*) provided cover for small mammals, which increased rates of seed predation rates from 60 to nearly 100%. Furthermore, if the seeds or foliage of dominant invasive species are unpalatable, this may increase rates of seed predation and herbivory on any remaining native plant species growing nearby (Orrock et al. 2008; Dangremond et al. 2010). Regardless, vertebrate seed and seedling predation may be a common mechanism underlying some of the declines in native plant species diversity, particularly woody species with larger seeds (Bartowitz and Orrock 2016).

Seasonal changes in population densities, resource availability, and perceived cover from predation may mitigate how recalcitrant invasive plant cover affects small mammals. Such findings suggest that, during certain seasons, the effects of an invasive plant on foraging activity may diminish. Barberry leaves were present during our entire study period. However, nonnative shrubs may leaf out earlier in the spring and senesce later in the fall than native species, thus extending the phenological window whereby these nonnatives provide small mammals a refuge. Nocturnal light intensity (Prugh and Golden 2014; Guiden and Orrock 2019) and the relative abundance of palatable seeds from canopy trees (Schnurr et al. 2002), neither of which were controlled for in this study, may also significantly impact small mammal foraging behavior. Predation risk may also vary with perceived food quality, as higher-quality resources can result in greater risk-taking (Utz et al. 2016). Therefore, the effects of recalcitrant invasive

species cover on small mammals may not be as strong during evenings with low moon luminescence, especially during heavy mast years.

Conclusion

Our findings highlight the potential for elevated foraging intensity in a key faunal assemblage resulting from invasive plants that form recalcitrant understories. Prior studies (Link et al. 2018, 2019) conducted in our field locations revealed depressed tree seedling densities under barberry but transplanted seedlings planted under barberry survived and grew at rates similar to control subjects. Such results, in combination with those presented here, suggest that small mammal foraging may be limiting recruitment of native trees or other heavily foraged plant taxa. Thick understory growth of *R. cathartica*, another invasive shrub spreading through temperature deciduous forests of North America, also elevates small mammal foraging rates and reduces the abundance of foraged native plants as a result (Guiden and Orrock 2017). However, very few studies have addressed such hypotheses despite the large number of invasive shrubs currently spreading through forest understories in North America and elsewhere.

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Appendix I

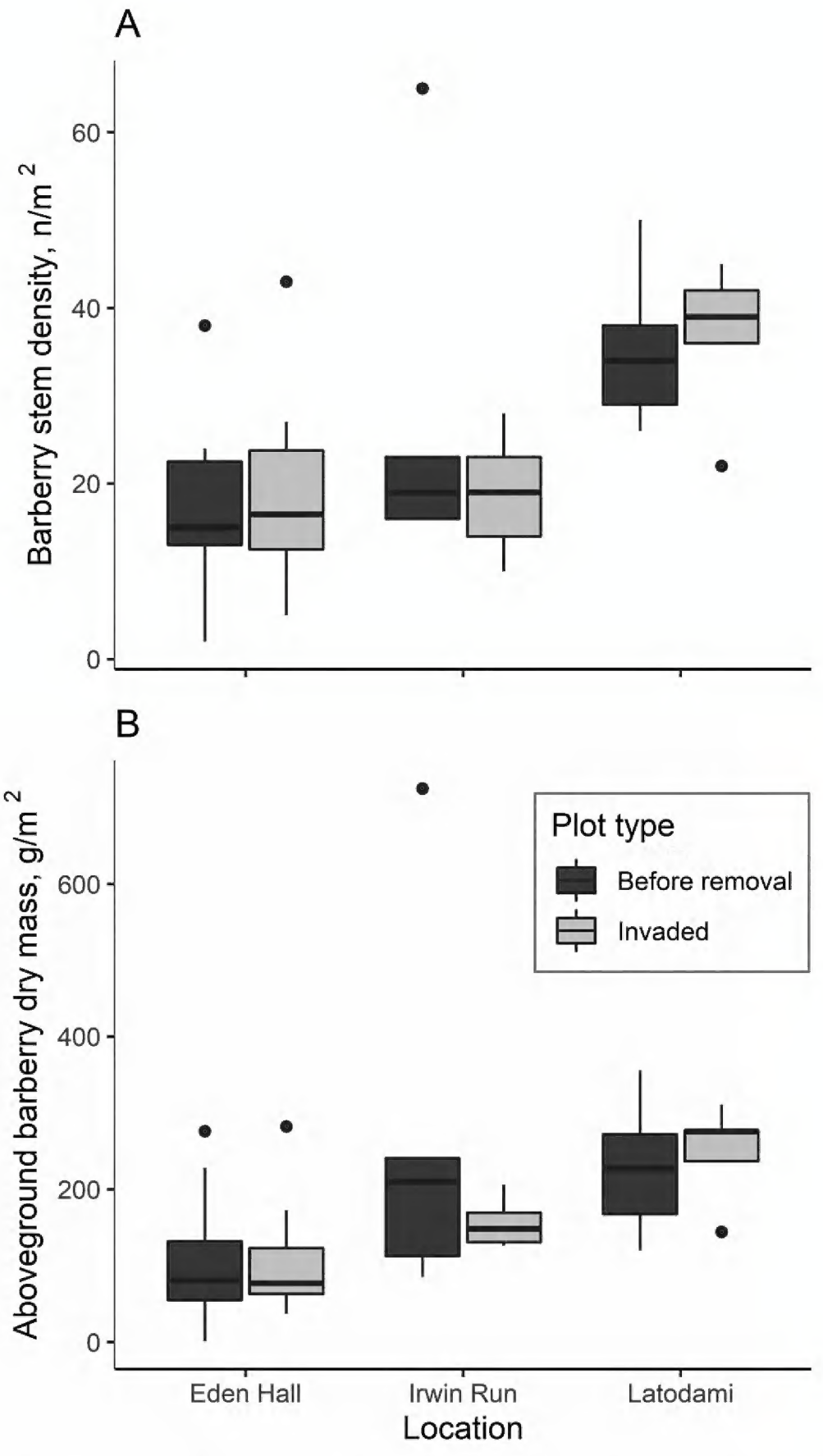

Figure AI. Distribution of **A** barberry stem densities and **B** barberry aboveground biomass in removal (prior to eradication) and invaded plot types, delineated by location. No barberry plants were recorded in control plots. Stem densities were assessed with a generalized linear model and Poisson error distribution; values significantly varied among locations ($\chi^2 = 87.4$, df = 2, $p < 0.0001$) but not plot types ($\chi^2 = 0.7$, df = 1, $p = 0.4175$). Barberry biomass was assessed with a linear model; values significantly varied among locations ($F_{2,36} = 5.7$, $p = 0.0073$) but not plot type ($F_{1,36} = 0.5$, $p = 0.4891$).